

NOTES ON THE OSTEOLOGY AND RELATIONSHIP OF THE FOSSIL BIRDS OF THE GENERA HESPERORNIS HARGERIA BAPTORNIS AND DIATRYMA.

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Our knowledge of the few Cretaceous birds that have been discovered in North America is very imperfect in spite of Professor Marsh's memoir on the Odontornithes; their origin and many points of their structure are still unknown and their relationship uncertain. By the kindness of Professor Williston, I am able to add a little to our knowledge of the structure of *Hesperornis gracilis* and *Baptornis advenus*, while the acquisition of a specimen of *Hesperornis regalis*, by the United States National Museum, enables me to add a few details concerning that species.

CRANIUM OF HESPERORNIS GRACILIS.

The example of *Hesperornis gracilis* belongs to the University of Kansas, and comprises a large portion of the skeleton, including the skull. Unfortunately the neck was doubled backward, so that the skull lay against the pelvis, while portions of dorsal and sternal ribs had become crushed into and intimately associated with the cranium, so that it was impossible to make out the shape of the palatal bones, provided even they were present. This was particularly unfortunate, as information as to the character of the palate of the toothed birds is greatly to be desired. Theoretically, the arrangement of the bones of the palate should be somewhat reptilian, or, if the struthious birds are survivals, the palate of such a bird as *Hesperornis* should present some dromæognathous characters. But, as was pointed out by D'Arcy Thompson, the skull of *Hesperornis regalis*, as described and figured by Marsh, differs very considerably from that of an ostrich, and the present specimen emphasizes or adds to the differences already noted. The presence of depressions for supraorbital glands and the size of the sagittal and lambdoidal crests neither denotes affinities with grebes and loons nor separation from struthious forms, since these characters are associated with aquatic and predatory habits and have no morphological value.

Owing to the crushed condition of the smaller bones and presence of numerous fragments of other parts associated with the cranium, it has proved impossible to ascertain the exact arrangement of the palatal bones, although it is apparent that this was quite different from that found among existing birds, either the Dromaeognathæ or Eurhipiduræ. While the head of the quadrate is undivided, the body of the

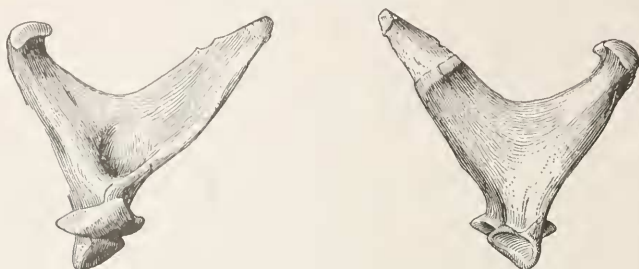


FIG. 1.—INTERNAL AND EXTERNAL ASPECT OF LEFT QUADRATE OF *Hesperornis gracilis*, $\times 1\frac{1}{2}$.

bone is slender and not overlapped and held in by a descending process of the squamosal; and these are important characters, especially the latter. The short, heavy quadrate of the Dromaeognathæ, locked in by the squamosal so as to be practically immovable, is a decidedly reptilian feature, eminently characteristic of the group and widely at variance with the conditions found in *Hesperornis*. The ascending or lachrymal process of *Hesperornis gracilis* is very long, quite unlike

that of *Hesperornis regalis* as described and figured by Professor Marsh.^a Just at its junction with the body of the quadrate there is a very evident articulation for the pterygoid.

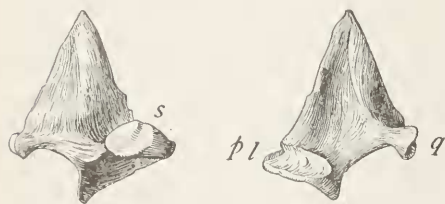


FIG. 2.—SUPERIOR AND INFERIOR VIEWS OF RIGHT PTERYGOID OF *Hesperornis gracilis*, $\times 1\frac{1}{2}$. *pl*, ARTICULATION OF PALATINE; *q*, ARTICULATION OF QUADRATE; *s*, ARTICULATION OF SPHENOID.

The pterygoid has much the same general shape as that of *Hesperornis regalis*, but differs from it slightly in details. It is a small, flat bone, roughly

rhomboidal in outline and with three articular surfaces, for the quadrate, basisphenoid, and palatine, as indicated on the accompanying figures. The most important of these is an elliptical facet at right angles to the body of the bone, for this is considered to be the facet for articulation with the basisphenoid, and this is connected with the question of the presence or absence of basiptyergoid processes. The entire under surface of the skull is considerably cracked and com-

^aDr. Beecher, who has kindly examined the Yale specimen, the original of Professor Marsh's figure, writes me that the process was naturally short and not the result of any breakage of the superior margin.

pressed, and at first sight there appeared to be no surface for articulation with the facet just mentioned. Close inspection, however, showed on the left side an apparent articular face of the proper size to receive the flat, articular portion of the pterygoid, though not projecting above the general level of the sphenoid. The basisphenoid of *Hesperornis* has thus absolutely nothing of the cruciform shape, due to the large, projecting basiptyergoid processes, so eminently characteristic of the *Dromæognathæ*.

Among the *Dinornithidæ*, *Emeus*, and *Meionornis* have comparatively short basiptyergoids, but even in these birds the processes project markedly above the level of the basisphenoid, while in *Hesperornis* this bone was in appearance not unlike the corresponding region of a loon, or penguin. The third articulation on the pterygoid would be for the palatine, but it is not easy to imagine the shape of a palatine that would fit such a surface and accord with the rest of the bones. The bone considered as a palatine by Professor Marsh is long and slender, with an articulation indicated on one side at about one-third the length of the bone; a somewhat similar, though imperfect, bone is present in the specimen of *Hesperornis regalis* belonging to the United States National Museum, but neither of these seems adjustable to the present pterygoid. In the present instance the pterygoid lay immediately over the left quadrate, but in spite of this intimate association, it appears probable that it is from the right side. With its point directed backward the supposed palatine articulation would be brought on the anterior side and in the proper position for union with the palatine and vomer. Such a disposition would give an arrangement of the bones of the palate somewhat analogous to that found in the Cassowary. The bone heretofore supposed to be a palatine may, perhaps, be the vomer, although it is difficult to account for the long portion back of the articulation. The vomer is said to have been double, and judging by the freedom of most of the bones of the cranium this may well have been the case. The bone figured as vomer in *Odontornithes* appears rather small for that of so large a bird as *Hesperornis regalis*. In the specimen of *Hesperornis gracilis* under consideration no bone representing the vomer can be made out, nor are there any evidences of the presence of maxillo-palatines.



FIG. 3.—SUPPOSED LACHRYMAL OF *Hesperornis regalis*. SLIGHTLY REDUCED.

By one of the curious chances of fossilization, the fragile sphenoid rostrum has been preserved. It is long and slender, and its anterior portion underlies and unites with the mesethmoid precisely as it does in *Urinator*, there being a further similarity between this genus and *Hesperornis* in the large size of the interorbital vacuity. This is very

unlike the condition prevailing among the Dromæognathæ, in which there is an extensive interorbital ossification.

Not only the component bones of the lower jaw, but the majority of those included in the cranium, appear to have been free from one another, with the exception of the premaxillæ. Whether this is due to the age of the individual or is a character common to the members of the genus *Hesperornis* can not now be decided; nor is it certain whether or not this freedom extended to the bones of the brain case, as the skull of *Hesperornis gracilis* has this portion still embedded in the matrix. In the Yale specimens the bones of the brain case appear to have been fused, although it is said that many of the other bones were free.

The example of *Hesperornis regalis* in the United States National Museum lacks the calvarium, but the bones of the jaw are quite free and so are two supposed to be the lachrymal and nasal, the former of which is here figured.

SHOULDER GIRDLE OF HESPERORNIS REGALIS.

Turning to the shoulder girdle, my own interpretation of this portion of the skeleton, based on material in the United States National Museum,^a differs somewhat from that given by Professor Marsh in the memoir on the Odontornithes, the most important points being the shape of the distal end of the clavicle and the fact that the scapula and coracoid do not lie practically in the same plane, but the angle formed by them is little more than a right angle, which is different from what is found among struthious birds. That the scapula and coracoid are quite free from one another and possess all the articular faces found in corresponding bones of birds of flight is, of course, well known.

While the open angle between the scapula and coracoid of struthious birds was used by Huxley as one of the diagnostic characters of the Ratitæ, it has come to be quite generally regarded as merely due to degeneration, and practically a question of mechanics; as the coracoid shortened the proximal end of the scapula would be lowered and the coraco-scapular angle opened, until with a greatly abbreviated coracoid the scapula was almost in line with it, as in *Casuaris*. That the coraco-scapular angle in *Hesperornis*, a bird with a vestigial wing, is less open than in the Dromæognathæ is perhaps still a question of mechanics. The struthious birds are heavy, short-bodied land birds, whereas *Hesperornis* was a long, lithe, proportionately slender-bodied diver, and unless the entire scapular arch was reduced the scapula could not be turned upward sufficiently to form an open angle with the coracoid. In this connection it may be noted that in *Rhea*, which has a rather long coracoid, the scapula is bent abruptly downward a short distance

^aThis specimen comes from the gray chalk, and the bones are but little crushed or distorted by pressure.

above its union with the coracoid in order to adapt itself to the curvature of the body. The suggestion may be made here that perhaps the ankylosis of scapula and coracoid which occurs among struthious birds may be of more value than is usually accorded it. This ankylosis occurs in these birds only, while the scapula and coracoid are in young birds suturally united as in dinosaurs.

The clavicle terminates distally in a small, slightly cup-shaped expansion which articulates with a small facet on the head of the coracoid. This is quite different from the description and figures in the *Odontornithes* where the clavicles are represented as pointed distally and articulating with the precoracoid process only, and I can only suggest that the specimens examined by Professor Marsh were slightly imperfect.

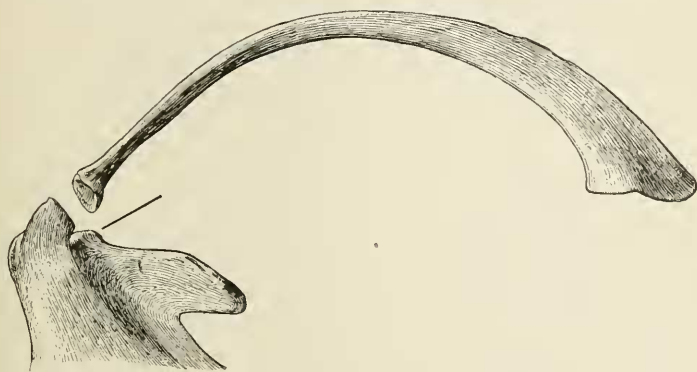


FIG. 4.—RIGHT CLAVICLE AND PART OF RIGHT CORACOID OF *Hesperornis regalis*, NATURAL SIZE. THE LINE SHOWS THE FACET FOR DISTAL END OF CLAVICLE.

The proximal ends of the clavicles appear to have been only slightly apposed, the major portion of the articulating surface being directed backward, probably for union with the anterior end of the sternum. We have in Harris's Cormorant a suggestion of how this condition of things may have been brought about, for in this flightless bird the keel of the sternum has aborted until its anterior end is even with the anterior end of the body of the sternum, and yet the keel still supports the clavicles as in other cormorants. This is an extremely good example of the retention of a morphological character while the entire pectoral girdle is undergoing degeneration and has ceased to be of use.

The relations of the bones of the pectoral arch in *Hesperornis* suggest that the conditions of the sternum in cormorants, where the keel is confined to the anterior portion, may represent a primitive type of sternum. Very similar conditions are found among the larger species of pterodactyls where the body of the sternum is smooth but a large anterior projection is present.

Following the description in *Odontornithes* Dr. Gadow^a writes that in *Hesperornis* the clavicles articulate with the precoracoid process only. Such a union can not be brought about in the specimen in the United States National Museum while, as said above, there is a very evident union between clavicle and coracoid as shown in figure 4. The importance of this is evident, for if the clavicles ended in a point and articulated only with the precoracoid the shoulder girdle would have a strikingly reptilian facies; as it is, the conditions are not very unlike those found among existing birds. The retention of a complete clavicle in a degenerate shoulder girdle is, however, an important point, for in modern birds with degenerate wings it is the proximal part of the clavicles which disappears, leaving the heavier distal portion attached to the coracoids. The complete separation of the clavicles and the fact that the proximal portion is much the heaviest is also a generalized condition.

The scapular arch of *Hesperornis* may be thus defined: Coracoid and scapula free from one another, preserving all articular faces, and forming little more than a right angle with one another; clavicles complete, free, without scapular process, and articulating with the coracoid. In struthious birds, on the other hand, the scapula and coracoid are ankylosed in the adult, bear only the humeral articulation, and form a very open angle with one another; clavicles absent or vestigial and represented by distal ends only.

In skull and shoulder girdle *Hesperornis* presents an interesting combination of characters, on the one hand showing generalized features and on the other close resemblances to modern birds. Thus we have in the Cretaceous a bird with a palatal structure quite unlike that of any struthious bird and with a vestigial wing which yet preserves many features found in the limbs of birds possessed of the power of flight. Add to this that no struthious bird is, as yet known, from North America,^b and we have an argument for those who believe that if birds did not have a diphylletic origin they at least divided into two very distinct branches early in their career.

In *Animals of the Past* attention was first called to the fact that the tarsi of *Hesperornis* were directed laterally outward almost at right angles to the body, instead of being directed downward as in other birds. This is brought about by the narrowness of the pelvis and straightness of the femur and by the outer and inner condyles of the femur being on the same level, instead of the outer being the lower of the two, as is usually the case among swimming birds. A similar arrangement, with similar results, is found in seals. From this position of the tarsi it would seem that the legs should naturally have been moved together, like a pair of oars, instead of alternately, although

^a Newton's Dictionary of Birds, p. 858.

^b See that part of this paper relating to *Diatryma*.

this may not have been the case. Having such a disposition of the legs combined with a total absence of external wings, *Hesperornis* must have been particularly awkward on land and probably came ashore as seldom as possible. Related to this peculiar position of the legs, it is suggested that the breeding habits must have been something like those of the grebe and loon and were such that at no time was the bird far from water. Even though *Hesperornis* was a marine bird, there is no reason why it could not have found plenty of suitable nesting places at once easy of access and yet beyond reach of the sea. That *Hesperornis* was a bird of cursorial habits before it took to the water is a supposition contradicted by every part of the skeleton. The elongate body, short femora, and great development of the outer

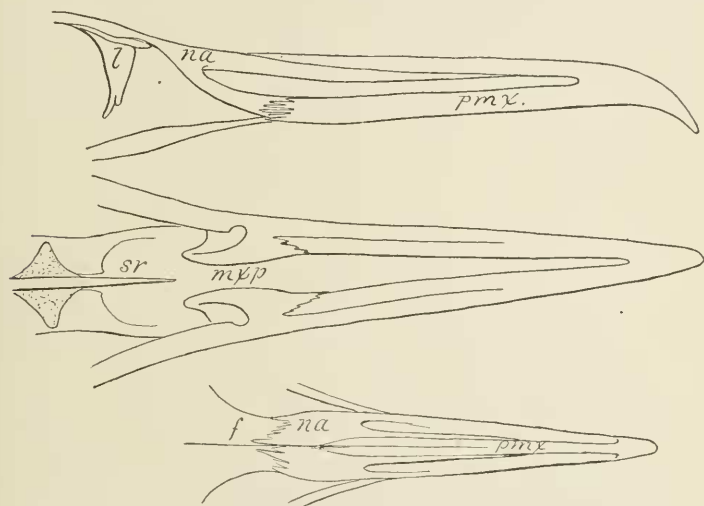


FIG. 5.—LATERAL, PALATAL, AND DORSAL VIEWS OF THE ANTERIOR PORTION OF THE CRANIUM OF A YOUNG CORMORANT, *Phalacrocorax urile*, SHOWING THE CHARACTER OF THE PALATE AND OF THE NARIAL OPENINGS. THE PALATINES HAVE BEEN REMOVED, ALL ENLARGED. *f*, FRONTAL; *l*, LACRYMAL; *mcp*, MAXILLOPALATINES; *na*, NASAL; *pmx*, PREMAXILLARIES; *sr*, SPHENOID ROSTRUM.

toe are all opposed to such an idea, and were other evidence required it is supplied by our present knowledge of the position of the legs.

A few words may, perhaps, be said here regarding the relationships of *Hesperornis*. The alleged colymbine affinities have never been apparent to me, those portions of the skeleton which are thought to indicate kinship with grebes and loons appearing to me as similarities of structure, connected with similarity of habits. There are many points of resemblance between *Hesperornis* and the cormorants, as well as between *Hesperornis* and the grebes, such as the shape of the tibia, the presence of a large patella pierced for the ambiens and functioning as a cnemial process, and the arrangement of the bones of the pectoral arch. As for the cranium, all these birds—*Hesperornis*, grebes, and cormorants—are holorhinal and schizognathous. In the cormorants

the nostrils are intermediate in form between a typical holorhinal and schizorhinal nostril, being elongate and posteriorly somewhat angular, while they lie well in advance of the posterior termination of the premaxillaries. That *Hesperornis* was schizognathous is, of course, uncertain. The figures accompanying this show the nostril and palate of a young nestling of *Phalacrocorax urile*, and similar conditions prevail in the young of *P. dilopus*. The desmognathism of the cormorants is clearly a secondary condition and is not brought about until some time after hatching. The closing of the nostril does not take place until very much later, or apparently just before the young takes to the water. As previously noted by Mr. Pycraft, a trace of the nostril remains in the shape of a minute orifice closed by horn. My own interpretation of the maxillo-palatines differs from that of Mr. Pycraft, a fact which I regret, as he is usually right; but, in the present instance, the maxillo-palatines are so clearly defined in the nestling that I have no choice in the matter. The collections of the United States National Museum include a large number of species of cormorants and a series of skulls representing individuals from the time of hatching up to shortly before the young take to the water, and it is upon this series that I have based my conclusions.

That *Hesperornis* should stand in the direct line of ascent of the grebes is, of course, quite out of the question, as it would imply the derivation of a modern bird of flight from a degenerate, flightless form. That the two may have had a common ancestor is an entirely different proposition, but if such be the case we must go far back in time to seek for this hypothetical form. And it must ever be borne in mind in dealing with birds that our knowledge of early forms is extremely slight, so that we have a very small foundation of facts for a very large edifice of theory, a pyramid resting on its apex, as it were. Our knowledge is indeed so limited that what we are pleased to term theory is really little better than speculation.

HARGERIA, new genus.

Hesperornis gracilis differs so much from its larger relative that it should be placed in a distinct genus, for which the name *Hargeria* is proposed in honor of Mr. Oscar Harger, who was one of Professor Marsh's assistants at the time of his investigations of the toothed birds, and, as noted in the preface to *Odontornithes*, rendered valuable aid in its preparation. The most important character is the size of the quadrate and length of the ascending process, and in birds this means much, as there is a remarkable constancy in the shape of this bone among related forms.

As contrasted with *Hesperornis* the genus *Hargeria* may be defined as follows: Quadrate with a large, upwardly directed lachrymal process; processes of nasals short; length of femur more than twice its greatest width across the head.

BAPTORNIS ADVENUS.

The skull of this bird is still unknown, so that we do not know positively whether or not it had teeth, although this is probably the case. Neither do we know the relationship between *Baptornis* and *Hesperornis*; both were flightless aquatic birds, but the structure of the limbs shows that at least they belong in separate families.

The body appears to have been stout, the neck long and slender, the individual vertebrae being much more elongate than in *Hesperornis*, approaching in this respect *Plotus* or *Podiceps*.

The vertebrae present, unfortunately, are not consecutive, a portion only of the cervicals being present, while some of the dorsals belong to the anterior portion of the series and others to the posterior part. The hypapophyses appear to have been developed, much as in *Hesperornis*, well forward in the dorsal region, in contrast to what occurs in modern water birds, such as penguins, auks, and loons, in which the hypapophyses begin immediately in advance of the sacrum and are longest about the middle of the series.

This would throw the center of effort farther forward in the old diving birds than in modern species, and may be due to the use of the muscles either while capturing fish or in moving about on land.

The synsacrum seems to have comprised ten vertebrae, but this is not certain, the first of which belongs to the dorsal series and bore a rib. The sacrum of *Hesperornis* contained fourteen vertebrae. Nothing of the pelvis is present save the anterior portion of an ilium, and this, although weathered, resembles the corresponding portion of the ilium of *Hesperornis*. The dorsal vertebrae were all free, and so were the ossa innominata in both *Baptornis* and *Hesperornis*, but this freedom is to be regarded as due to the aquatic habits of these birds and not as morphological characters. While the bones of aquatic animals are heavier than are those of land animals, ossification and union between contiguous parts takes place much more slowly, and in such strictly aquatic birds as the penguin and great auk the dorsal vertebrae and ossa innominata are similarly free.

The coracoid is rather wide and thin, much longer than that of *Hesperornis*, and apparently without a precoracoid process or perforation; an articulation is present for the reception of the clavicle, but this latter bone was not preserved.

Only the proximal portion of one scapula, the left, is present; this indicates a stout bone, and there is a suggestion that it may have expanded distally, as in penguins, but this is suggested, nothing more.

The humerus is short, round in section, and considerably curved, as in *Apteryx*. Although the proximal end is lacking, it seems to have been not far from 4 inches (100 mm.) long. The radius and ulna are extremely short, measuring but three-fourths inch (20 mm.) in length.

The extraordinary thing about them is that short as they are they are perfectly formed and possess the muscular insertions of much larger bones, while it is evident that the bones of the manus were also present.

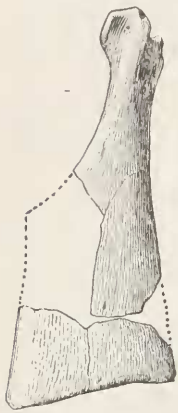


FIG. 6.—RIGHT CORACOID AND PORTION OF LEFT SCAPULA OF *Baptornis advenus*, NATURAL SIZE.



This is quite different from *Hesperornis*, in which the humerus is rather long and straight, and the bones of the forearm and manus absent; it carries to an extreme conditions found in the great auk, a bird in which the forearm is much reduced, though still functional. *Baptornis* thus presents the peculiarity of a forearm of diminutive size, whose bones are perfectly formed, bear the muscular impressions of much larger wing bones, and imply the presence of quill feathers, and not improbably the use of the wings in conjunction with the feet in aquatic locomotion. In other birds in which the wings have

undergone extensive reduction, such as *Rhea* and *Struthio*, to say nothing of *Apteryx*, the radius and ulna lack the well-defined form and muscular ridges of *Baptornis*.

The femur, while short and stout, has nothing of the squareness shown by *Hesperornis*, but resembles rather that of a loon on a more massive scale. The greater trochanter is slightly raised above the level of the head of the femur, and the outer condyle extends below the level of the inner; the antitrochanter also appears to have looked slightly downward, so that the position of the leg in swimming was doubtless like that of existing waterfowl. This is the ordinary arrangement and would not be specially mentioned but for the fact that it is the reverse of these conditions, coupled with the character of the tibio-tarsal joint that causes the tarsus of *Hesperornis* to stand out almost at right angles to the body. The procnemial process of the tibia is higher than in *Hesperornis*, and the large patella appears to have articulated on one side of this, somewhat as in grebes, and not as in penguins and cormorants, where the patella functions as a cnemial process. The patella is large, of a modified trihedral form, and has a large perforation for the ambiens. The taxonomic value of such a perforation is lessened by the fact that among cormorants such a perforation is present in some species and absent in others, and while this may prove to be correlated with other characters the available material does not show this.



FIG. 7.—LEFT HUMERUS, RADIUS AND ULNA OF *Baptornis advenus*, NATURAL SIZE.

The tarsus is stout and somewhat compressed laterally; although weathered there appear to have been no tendinal grooves, much less any tendinal foramina, these last marking a degree of tarsal specialization vastly higher than was possessed by any Cretaceous bird. If it is permitted to borrow a little of the style of W. K. Parker it might be said that the early birds show a great deal of reptilian coarseness in their articulations, and lack the detail and sharpness of finish that came later and marks a higher degree of specialization. The lower end of the tarsus bears a faint imprint of the presence of the small first digit, but still as much as exists in some ducks. The phalangeal articulations are narrow, indicating compressed digits; this is also shown by the proximal fragment of a median digit. Compressed digits are now associated with lobate feet, and thus, so far as we know, the lobate foot preceded the webbed foot in point of time. Our knowledge of early birds is, however, so trivial that it is scarcely worth while to make any generalizations on this subject, the more that there is no reason why the two types of foot may not have been evolved



FIG. 8.—RIGHT PATERA OF *Baptornis advenus*, NATURAL SIZE.

independently of one another. The waders indeed suggest that the evolution was independent, as this group shows the beginning of such feet in such forms as the phalarope and avocet.

In the length of the coracoid and absence of a precoracoid process; in the existence of a complete though greatly reduced wing; the shortness of the sacrum; proportions of the leg bones and position when in use, *Baptornis* is very different from *Hesperornis* and more like existing birds. In the slender cervicals, arrangement of tibia and patella, and general structure of the leg *Baptornis* is more like a grebe than is the contemporary *Hesperornis*, and if, with the small amount of material available, it is deemed essential to establish any connection between groups of existing and fossil birds it is suggested that the ancestors of *Baptornis* are much more likely to have been also the progenitors of the Colymbine group than are those of *Hesperornis*.

It is certain, as said near the beginning of the notes on *Baptornis*, that this bird belongs in an entirely different family from *Hesperornis*, and if it is ever given to us to know more of the bird it may prove to belong in a separate order.

THE POSITION OF DIATRYMA.

Diatryma gigantea, from the Eocene of New Mexico, was placed with the struthious birds by Professor Cope, mainly, it would appear, on account of its size, since he points out some differences between the tarsus and that of the ostrich and emeu, and notes resemblances between the distal articulations and those of *Gastornis*. At the time *Diatryma* was described the great South American *Stereornithes* had not been discovered or Professor Cope would doubtless have instituted comparisons between them and *Diatryma*.

Unfortunately, the type and only specimen of *Diatryma* is a fragmentary tarsus, while the only material at hand representing the *Stereornithes* is an indifferent cast of *Brontornis*. Still there are sufficient resemblances between the two to warrant the suggestion that if material comes to light it will be found that the affinities of *Diatryma* are with the *Stereornithes* and not with the *Dromæognathæ*.

There is nothing more improbable in the North American origin of the *Stereornithes* than in the similar origin of the large edentates and llamas, both of which are subscribed to.

For the present there seems to be no evidence of the occurrence of any large dromæognathous bird in North America, and the presence of the tinamous may be regarded as the northward extension of a southern fauna.